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The effect of salt (NaCl) stress on the ultrastructure of mesophyll and bundle sheath cell chloroplasts and the activity of superoxide dismutase in maize plants (*Zea mays* L.)

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The activity and isoenzyme content of superoxide dismutase (SOD) and changes in the leaf ultrastructure have been studied comparatively in chloroplasts of mesophyll and bundle sheath cells isolated from maize plants (*Zea mays* L.) grown in an artificial climate chamber at various concentrations of NaCl (0 mM, 50 mM, 100 mM, 200 mM). The SOD activity was found to increase in plants exposed to 50 mM and 100 mM NaCl, but at 200 mM NaCl it was partly inhibited. The study of the isoenzyme activity of SOD revealed Fe-SOD isoform, which intensity increased with enhancing salt concentrations. The analysis of the ultrastructures of mesophyll (M) and bundle sheath (BS) cell chloroplasts by electron microscopy showed that chloroplasts of M cells were sensitive,whereas chloroplasts of BS cells were tolerant to stress. At the high salt concentration (200 mM), a partial transition of the agranal structure of BS cell chloroplasts to the granal structure occurred.

***Keywords**: Zea mays* L., *salt stress, superoxide dismutase, mesophyll, bundle sheath, chloroplast, ultrastructure*

INTRODUCTION

Maize plants (*Zea mays* L.) use C_4 photosynthetic pathway for the assimilation of CO_2 and this process is divided into two cycles. This division within the leaf is implemented by two specialized photosynthetic cells: M cells surrounded BS cells, located compactly around the veins. BS and M cells differ in their metabolic functions in the maize plant: PEP-carboxylase and C_4 photosynthesis function in M cells, whereas RBP carboxylase and Calvin cycle function in BS cells (Raines, 2003, von Caemmerer and Furbank, 2003). M cell chloroplasts of maize leaves have a granular structure and they possess all components of the electron transport chain, which ensures the photochemical functioning of PS I and PS II. In contrast, the granular structure is not clearly visible in BS cell chloroplasts where mainly PS I functions. Electron microscopy studies revealed differences between the structures of M and BS cells. Thus, M cells are characterized by granal structure, stromal thylakoids and small amounts of starch granules, whereas BS cells are distinguished by their agranal structure and a greater amount of starch granules (von Caemmerer et al., 2003, Shao et al., 2015)

Currently, changes in the molecular, membrane and cellular levels are brought to the fore in the study of the response of living organisms to various extreme conditions. During long-term and intense stress, oxidation of free radicals occurs in the cell (Ramegowda and Senthil-Kumar, 2015). One of the initial responses to stress is the lipid peroxidation process induced by the formation of reactive oxygen species (superoxide anion radical, $O^{2.-}$, - H_2O_2, etc.). Chloroplasts and peroxisomes are the main places for the formation of reactive

oxygen species (ROS) (Asada, 2006). Oxidative stress is often accompanied by photoinhibition. On the other hand, a correlation between the activity of antioxidant enzymes and the inhibition degree of the photosynthetic apparatus was established (Gadjev et al., 2006). Enzymatic antioxidants such as superoxide dismutase (SOD), ascorbate peroxidase (APO) and catalase (CAT) are the main components of the cell antioxidant defense system.

Superoxide dismutase is known to catalyze the reduction of superoxide radical to hydrogen peroxide: $\cdot O_2 + O_2^- + 2H^+ = H_2O_2 + O_2$

Based on recent reports, SOD molecules have several isoforms differing in their cellular localization, primary structure, molecular mass and nature of the metals in the active center – Cu/Zn-SOD, Mn-SOD and Fe-SOD (Alscher et al., 2002; Gill and Tuteja, 2010; Mahanty et al., 2012). Cu / Zn-SOD (30-33 kDa) was found mainly in the cytosol, mitochondria, peroxisome; Mn-SOD (75-94 kDa) - in mitochondria, peroxisome; Fe-SOD (36-48 kDa) - in chloroplasts and cytoplasm of some legumes. Superoxide dismutase was revealed in various organisms, including plants (Kumar et al., 2013). Contrary to SOD in animal cells, plant SOD is distinguished by its numerous isoenzymes. As a result of multiple investigations, it has been found that during the plant protection from oxidative stress, the SOD activity changes depending on the plant species, the stage of development and the degree of the stress effect (Alscher et al, 2002).

The main purpose of the study was to determine the effects of various concentrations of NaCl on the ultrastructure of chloroplasts isolated from mesophyll and bundle sheath cells and the activity of superoxide dismutase in maize leaves.

MATERIALS AND METHODS

Material: Seedlings of the maize plant (*Zea mays* L.), which is a cereal crop, were cultivated in the hydroponic growing mediums – Knop's solution. Seeds were transferred to the filter paper wrapped in roll after being sterilized in 2.5% $KMnO_4$ solution for 15 min. The seeds were germinated in the nutrient medium containing various NaCl concentrations (0 mM, 50 mM, 100 mM, 200 mM NaCl), for 14 days, with a photoperiod of 12h/12, at 25ºC. At the same time, plants grown in soil under phytotron conditions were also used (photoperiod – 14 h/10 h, t – 26ºC, light intensity - 3000 lux).

Isolation of subcellular fractions of chloroplasts from mesophyll and bundle sheath cells: Maize seedlings were used in the experiments after the complete maturation of the second leaf. The plants were exposed to salt stress (0 mM, 50 mM, 100 mM, 200 mM) for 5 days. The differential centrifugation method was used to isolate subcellular fractions (chloroplasts, etc.) from mesophyll and bundle sheath cells of leaf samples. To obtain assimilating tissues, leaves were detached from stems, washed with distilled water and cut into small segments 2-3 mm wide. These segments were homogenized in 25 mM HEPES buffer (pH 7.8) containing 0.3 M sucrose, 1 mM EDTA, 15-20 mM 2-mercaptoethanol (buffer A) using MPW-302 (Poland) mechanical disintegrator, for 4 sec, at 7000 rev/min.

The homogenate obtained was filtered through 4-fold capron and then throughthe Shotov funnel with a pore diameter of 80 μm. The obtained filtrate contained only M cells, the residual part called pulp contained a mixture of M and BS cells. The filtrate was centrifuged for 15 min, at 300 g. The obtained supernatant contained the cytosolic fraction of M cells, whereas the pellet was the chloroplast fraction.The obtained pellet was washed with a buffer A. Then 10 ml of the buffer A without sucrose was added and centrifugation was performed for 15 min, at 300 g. The pellet remained in the filter (pulp) was washed several times with the buffer A, suspended and then homogenized first for 60 sec, at 6000 rev/min and then for 80 sec at 8,000 rev/min. The obtained filtrate was applied to the Shotov funnel with 211 μm diameters of pores. The obtained filtrate contained a mixture of homogenates of M and BS cells. The pellet was suspended in the buffer A and homogenized for 60 sec, at 6,000 rev/min and then for 15 sec, at 8,000 rev/min. The filtrate was centrifuged for 20 min, at 10,000 g. The obtained supernatant contained the cytoplasm of BS cells, whereas the pellet contained chloroplasts of BS cells (Guliev et al., 2003). The pellet was suspended in the buffer A without sucrose, then centrifuged for 20 min, at 10,000 g. This resulted in the

separation of the membrane and stroma of the chloroplasts. All experiments were performed in a cold room with a temperature of 4ºC.

Determination of superoxide dismutase using the spectrophotometric method: The enzyme activity was determined at 450 nm using SOD Assay Kit (Sigma, Aldrich). The enzyme activity was found to be higher in BS cells compared with M cells.

Determination of the isoenzyme content of superoxide dismutase: Electrophoresis on 10% native polyacrylamide gel (PAGE), for 3h, at 4ºC and direct current (30mM) using Tris-glycine (pH 8.3) buffer was performed for the analysis of the isoenzyme content of SOD in maize leaves. After electrophoresis, gel was stained in the darkness for 30 min in 100 ml 1.0 M Tris-HCl (pH 8.2) buffer containing 10 mg NBT, 75 mg EDTA-Na and 3 mg riboflavin.

Ultrastructure of mesophyll and bundle sheath cells: Ultrastructure of M and BS cells were studied using the electron microscope in the 2nd leaves of the maize plant cultivated under artificial climate conditions. The samples were fixed in 0.1 M phosphate buffer (pH 7.4) containing 2% paraformaldehyde, 2% glutaraldehyde and 0.1% picric acid. The samples were kept in the fixative solution for at least one day, then postfixed for 2 hours, in 1% osmium tetroxide solution prepared in phosphate buffer (pH 7.4). Araldite-Epon blocks were made from the material based on general protocols adopted in electron microscopy (Kuo, 2007). Ultra-thin sections (1-2 µm) were made with an ultramicrothome Leica EM UC7, stained with methylene blue, azure II, and basic fuchsin or toluidine blue. Promo Star (Zeiss) microscope was used and the necessary parts were photographed with a Canon D650 digital camera (D'Amico, 2005). The 50-70 nm ultra-thin sections from the same blocks were first stained with 2% uranyl acetate solution, then with 0.6 % pure lead citrate prepared in 0.1 N NaOH solution. Ultra-thin sections were investigated on the electron microscope JEM-1400 at a voltage of 80-120 kw and electronograms were obtained. Morphometric analysis of the image was carried out with TIF format electronograms using computer software (The TEM imaging platform) developed by the German company "Olympus Soft Imaging Solutions Gmbh".

Statistical analysis was performed in 3 biological replicates using the computer program Excel 2016.

RESULTS AND DISCUSSION

Spectrophotometric analysis of mesophyll and bundle sheath cells revealed a higher SOD activity in BS cells compared with M cells (Figure 1). As seen in the figure, the SOD activity did not increase markedly in M and BS cells of the plants grown at 50 mM NaCl compared with the control. However, a significant enhancement in the enzyme activity (55% and 69%, respectively) was observed in both subcellular fractions at 100 mM NaCl and the activity decreased at 200 mM concentration of salt. The enzyme functioning resulted in the formation of the reactive oxygen species H_2O_2, which amount enhanced in the plant cells with the increasing salt concentration. As H_2O_2 is an inhibitor of SOD, its excessive accumulation in the cell at the high salt concentration (200 mM) led to partial inhibition of the enzyme (Jalali-e-Emam et al., 2011) (Figure 1). Omoto et al. (2013) obtained similar results. According to the authors, after emerging the 4th leaf, maize seedlings were watered for 5 days with 3% NaCl solution, which resulted in an increase in the SOD activity both in M and BS cells compared with the control. Whereas, activities of glutathione reductase and monodehydro reductase were observed only in the mesophyll. The ascorbate peroxidase activity and the total amount of ascorbic acid were higher in BS cells exposed to salt stress. According to Hasan et al. (2015), the structure of mesophyll cells in NADP-malic enzyme type (NADP –ME) C_4 plants are more sensitive to salt stress compared with that of bundle sheath cells.

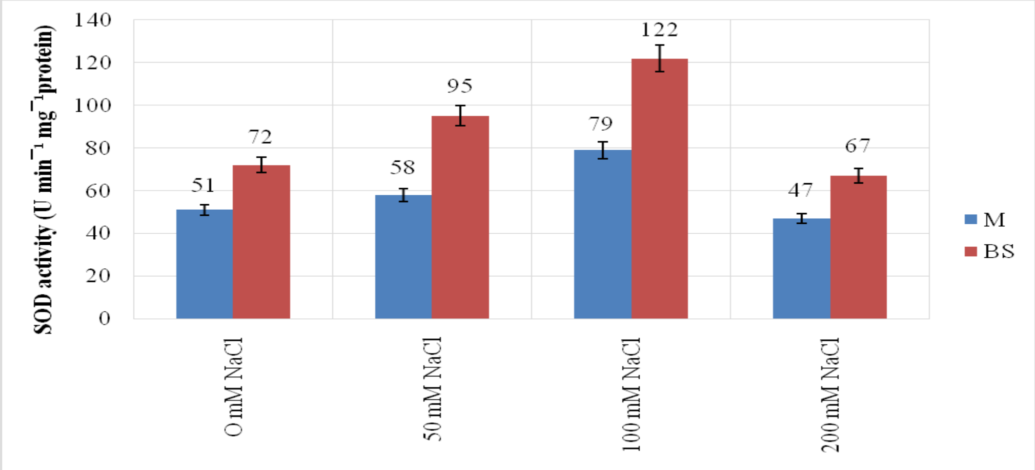


Fig. 1. Changes in the SOD activity in mesophyll and bundle sheath cells of the maize plant depending on the NaCl concentration.

Electrophoretic analysis of mesophyll and bundle sheath cells revealed 1 isoform of the enzyme in BS cells. (Figure 2). Based on literature data, this isoform is suggested to be Fe-SOD (Menezes-Benavente, et al., 2004). As seen in the figure, the isoform intensity increased depending on the salt concentration.

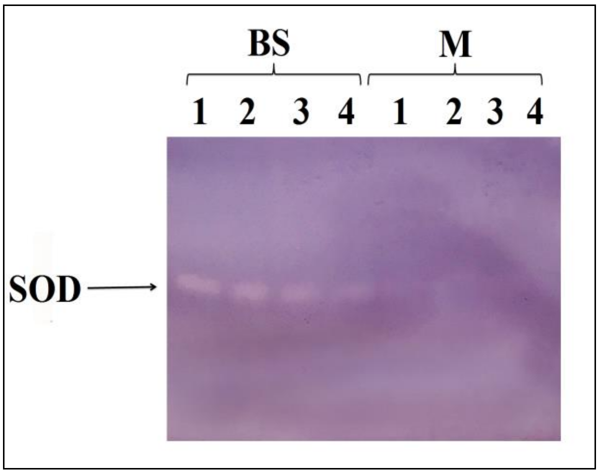


Fig. 2. Isoenzyme content of superoxide dismutase in M and BS cells of the maize plants grown at various NaCl concentrations: 1- 200 mM NaCl, 2 - 100 mM NaCl, 3 - 50 mM NaCl, 4 - 0 mM NaCl.

Changes in the ultrastructure of chloroplasts were analyzed using the electron microscope in leaves of the maize plant grown at various concentrations of NaCl (0 mM, 50 mM, 100 mM, 200 mM) (Figure 3A-D). Mesophyll cell chloroplasts of plants grown under normal conditions have a thylakoid membrane with a well-developed granal structure and a small amount of lipid droplets (plastoglobules) (Figure 3A). Granal thylakoid membranes surrounded by thylakoid membranes, lamellae connecting them and 8 lipid droplets are clearly seen in Figure 3A. Some authors reported the existence of starch granules (Hasan et al. 2005, 2006). But according to electronograms obtained in our research, there is no starch granules in the stroma of the mesophyll cell chloroplasts. As seen in Figure 3B-D, the structure of mesophyll chloroplasts was damaged and swollen after exposure to salt, with the following destruction of the thylakoid membranes (Figure 3). Along with the above ultrastructural changes, chloroplast integrity (external and internal membranes) was also destroyed (Figure 3D). Similar results were obtained by other researchers (Hasan et al. 2005, 2006).

Figure 4 shows changes in the ultrastructure of BS cell chloroplasts of maize plants exposed to salt (NaCl) (4B-D) and in leaves of the control plants (4A). As can be seen, BS cell chloroplasts of the maize plant have a typical NADP-ME structure. As in C_4 plants,they have thylakoid membranes with arganal structures and lipid droplets occur in the stroma (white and black arrows in Figure 4A). It has been established that there is no apparent damage to the thylakoid membrane

system of the BS cell chloroplasts due to salt exposure.The structures of the thylakoids are not destroyed with the increasing salt content (Figure 4B-D). But the volume and number of the lipid droplets increase multiple times (black arrows in Figure 4C, D). It should be noted that salt stress causes a change of the agranal structure to the granal structure in BS cell chloroplasts (white bold arrows in Figure 4C, D).

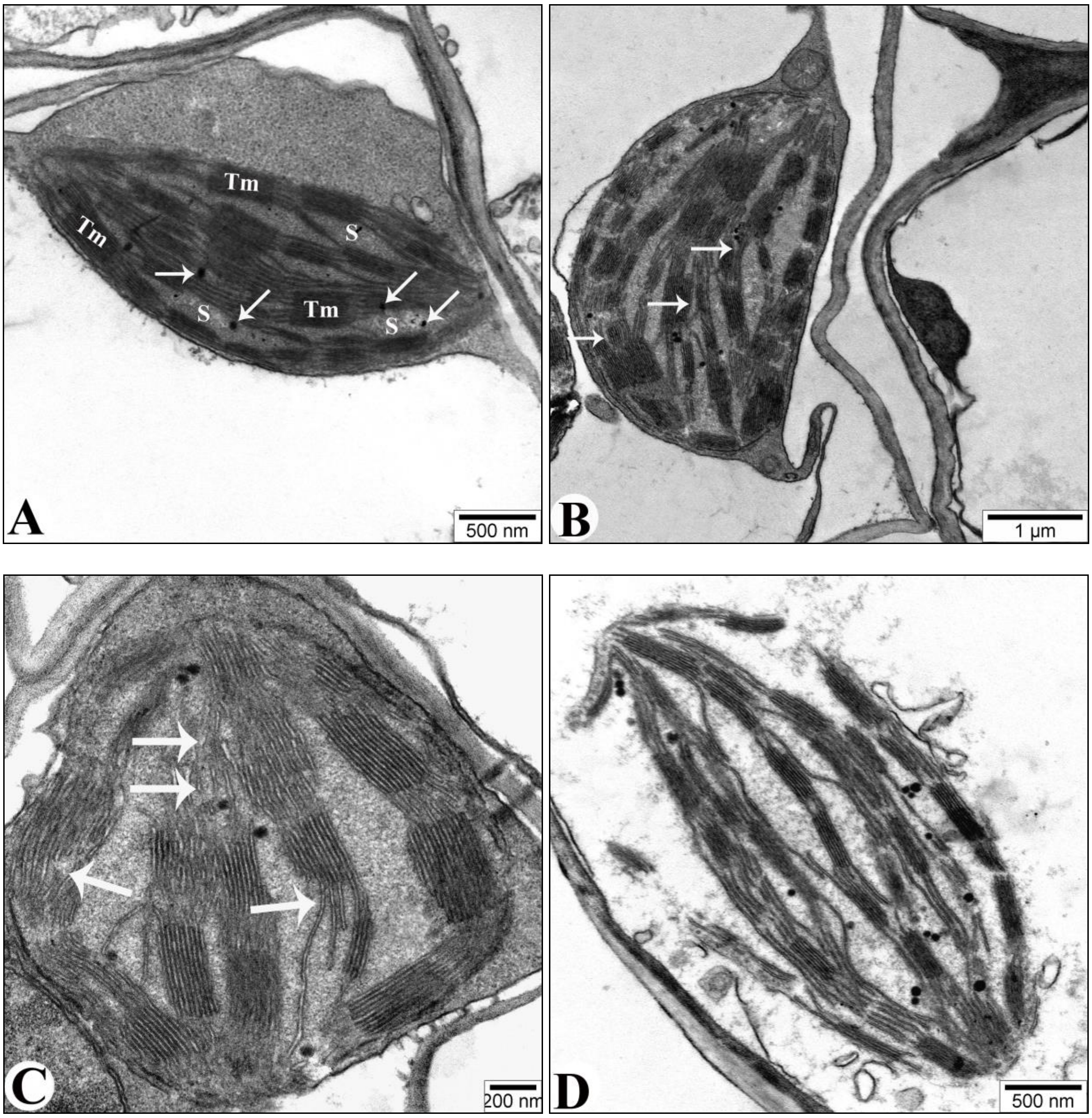


Fig. 3. Ultrastructural changes in mesophyll cell chloroplasts of maize plants exposed to salt stress (B-D) compared with the control group (A). B - 50 mM NaCl; C - 100 mM NaCl; D - 200 mM NaCl; Abbreviations: Tm-thylakoid membrane, S-stroma, white arrows in 3A-lipid droplets (plastoglobules), white arrows in 3B and 3C-formation of spaces between thylakoid membranes with granular structures and damage to the membranes. A-D-Electronograms of ultra-thin sections (50-70 nm). Stain- uranyl acetate and pure lead citrate. The explanation is in the text.

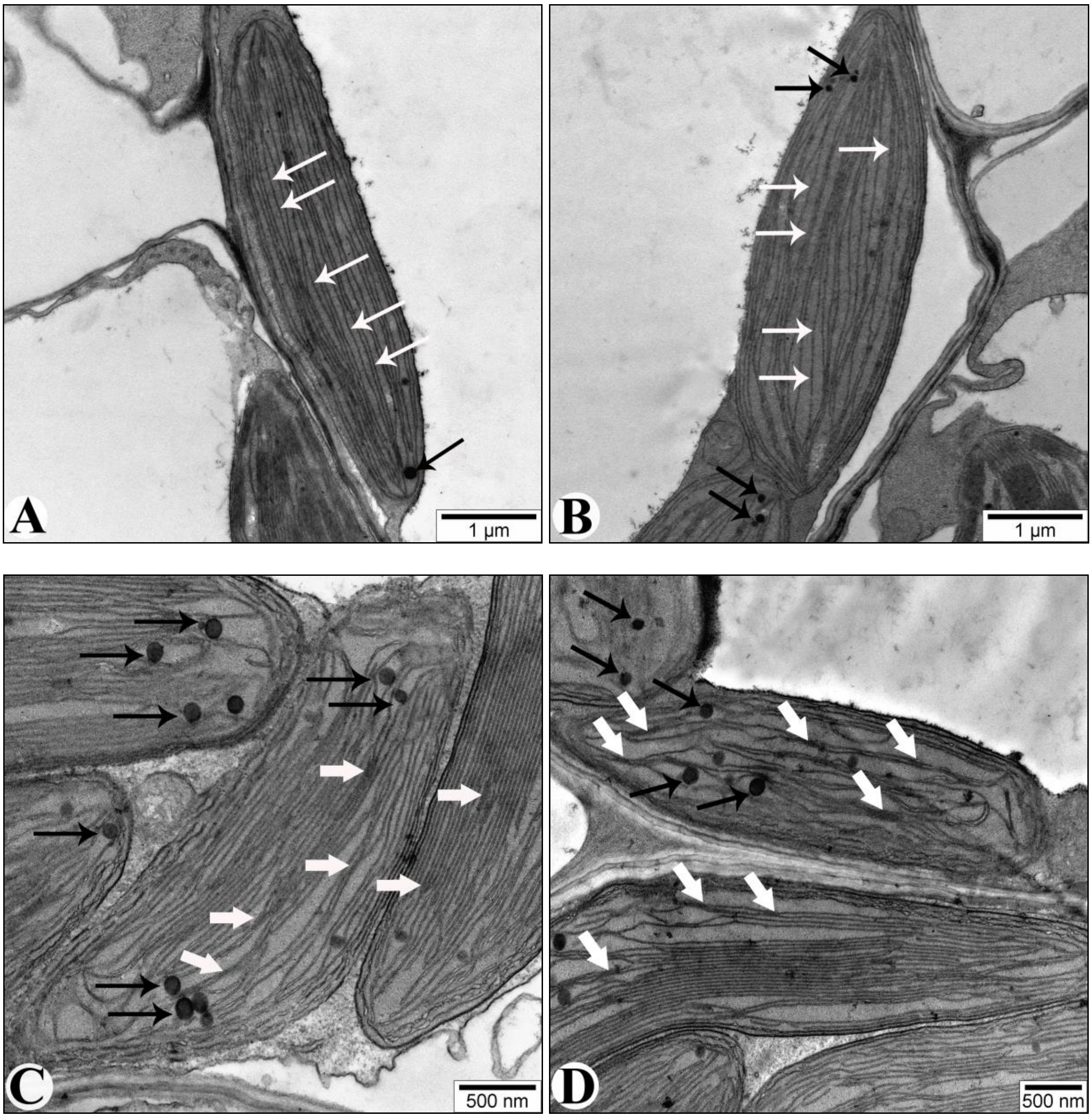


Fig. 4. Ultrastructural changes in bundle sheath cell chloroplasts of maize plants exposed to salt stress (B-D) compared with the control group (A). B - 50 mM NaCl; C - 100 mM NaCl; D - 200 mM NaCl; White arrows in A and B - thylakoid membranes having a granular structures. Black arrows in A, B, C and D - lipid droplets (plastoglobules), Bold white arrows in C and D - zones of the transition of the agranal thylakoid membranes to the granal ones. A-D - Electronograms of ultra-thin sections (50-70 nm). Stain-uranyl acetate and pure lead citrate. The explanation is in the text.

According to the results obtained from the studies, as well as the literature data, M cell and BS cell chloroplasts of C_4 plants contain granal and stromal lamellae, which differ greatly in their biochemical composition, function and localization in the cell. It was found that at low salt concentrations, the activity of SOD - one of the main components of the antioxidant defense system in the cell - enhanced relative to the control. However, at 200 mM concentration of salt, the enzyme activity was partly inhibited. One isoform of the SOD enzyme was observed in BS cells, contrary to M cells. The intensity of this isoform was shown to increase with increasing salt concentrations.

The results of the experiments showed that SOD localized in BS cells plays a major role in the adaptation of maize plants to salt stress. The ultrastructure of chloroplasts in salt-exposed maize leaves was analyzed by electron microscopy. The structure of M cell chloroplasts was shown to be damaged due to salt exposer. They became swollen which led to the destruction of thylakoid membranes. However, there was not such a change in the thylakoid membrane system of BS cell chloroplasts and even apartial transition of the agranal structure to the granal structure occurred.

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Duz (NaCl) stresinin qarğıdalı bitkisinin (*Zea mays* L.) mezofil və örtüktopa hüceyrələrində xloroplastların ultrastrukturuna və superoksiddimutaza fermentinin aktivliyinə təsiri

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Təqdim olunan işdə NaCl duzunun müxtəlif qatılıqlarında (0 mM, 50 mM, 100 mM, 200 mM) suni iqlim kamerasında becərilən qarğıdalı bitkisindən (Zea mays L.) ayrılmış mezofil və örtüktopa hüceyrələrinin xloroplastlarında superoksiddismutazanın (SOD) aktivliyi, izoferment tərkibi və yarpağın ultrasrukturunda baş verən dəyişikliklər muqayisəli öyrənilmişdir. Aparılan tədqiqatlar nəticəsində müəyyən olunmuşdur ki, stresin təsirindən SOD-un aktivliyi kontrola nisbətən duzun 50 mM və 100 mM qatılığında artmış, lakin 200 mM qatılığında fermentin fəallığı qismən inhibirləşmişdir. SOD fermentinin izoenzim tərkibinin təyini zamanı örtüktopa hüceyrələrində 1 izoforması (Fe- SOD) müşahidə edilmişdir və müəyyən edilmişdir ki, duzun qatılığı artdıqca izoformanın intensivliyi artır. Elektron mikroskopu vasitəsilə mezofil (MH) və örtüktopa hüceyrələri (ÖTH) xloroplastlarının ultrastrukturunun tədqiqi zamanı mezofil xloroplastlarının stresə qarşı daha həssas, ÖTH xloroplastlarının isə nisbətən davamlı olduğu müəyyən olunmuşdur. Duzun yüksək qatılığında (200 mM) ÖTH xloroplastlarının aqranal qurluşunun qismən qranal quruluşa keçməsi aşkar edilmişdir.

***Açar sözlər**: Zea mays L., duz stresi, superoksiddismutaza, mezofil, örtüktopa, xloroplast, ultrastruktur*

Влияние солевого (NaCl) стресса на ультраструктуру хлоропластов клеток мезофилла и обкладки проводящих пучков и активность фермента супероксиддисмутазы в растениях кукурузы (*Zea mays* L.)

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В представленной работе было проведено сравнительное изучение активности и состава изоферметов супероксиддисмутазы (СОД) хлоропластов клеток мезофилла и обкладки проводящих пучков, выделенных из растения кукурузы (*Zea mays* L.), выращенной в камере искусственного климата при различных концентрациях NaCl (0 mM, 50 mM, 100 mM, 200 mM), и изменений, происходящих в ультраструктуре листьев. В ходе проведенных исследований было обнаружено, что активность СОД под воздействием солевого стресса при концентрациях NaCl 50 mM и 100 mM возрастала по сравнению с контролем, однако при концентрации соли 200 mM активность фермента частично ингибировалась. При определении состава изоэнзимов была обнаружена 1 изоформа фермента СОД (Fe-SOD) и выявлено, что при повышении концентрации соли интенсивность изоформы возрастает. С помощью методов электронной микроскопии при исследовании ультраструктуры хлоропластов клеток мезофилла и обкладки проводящих пучков было обнаружено, что хлоропласты мезофилла более чувствительны к стрессу, чем хлоропласты обкладки. Также выявлено, что при высокой концентрации соли (200 mM) агранальная структура хлоропластов обкладки частично переходит в гранальную структуру.

Ключевые слова: Zea mays L.*, солевой стресс, супероксиддисмутаза, мезофилл, обкладка проводящих пучков, хлоропласт, ультраструктура*

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